DIANTHOVEUS: A NEW GENUS OF CYCLANTHACEAE[1]

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ABSTRACT

Dianthoveus cremnophilus, a terrestrial Cyclanthaceae from southwestern Colombia to northern Ecuador, is described as a new genus and species. The cupules at the base of the stamens and the long, narrow, moderately flattened seeds are unique. Cladistic analysis supports the hypothesis that leaf idioblasts with randomly oriented styloids (leaves scabrous when dry), root styloids, sessile anthers, and inaperturate pollen are synapomorphies with the widespread, monospecific *Evodianthus*. The new genus differs fundamentally from *Evodianthus* by having a uniseriate staminate perianth and in seed shape and seed coat structure. *Dianthoveus* shares additional uncommon characters with *Evodianthus* (e.g., separate fruits, terminal inflorescences, symmetrical flowers) that are not unique in the family. With *Schultesiophytum* it shares some of these uncommon characters but uniquely shares only laminar anther appendages. Although *Dianthoveus* and *Dicranopygium* subgenus *Gleasonianthus* uniquely share staminate flowers with eglandular tepals, no other characters suggest a close relationship between them.

Exploration of tropical wet forests in southern Central America and northwestern South America in recent years has greatly increased the number of collections and species known from these areas. This was especially predictable for the Cyclanthaceae, which are restricted to the wettest, often least-explored habitats (Grayum & Hammel, 1982). Since the time of Harling's (1958) monograph, which included 178 species in 11 genera, 29 new species have been added to this predominantly epiphytic family. More than 30 additional new species are now known from Central America and the Chocó region of South America alone (Hammel, unpubl.). However, only one new subgenus (Wilder, 1978) and no other supraspecific taxa have been described. In fact, in recent years only 10 genera have been recognized; *Pseudoludovia* is thought to be a mixed collection: a spadix, perhaps of a *Sphaeradenia*, and leaves of *Ludovia* (Wilder, 1978). Harling suggested that on further study it might be possible and logical to subdivide the three largest genera into additional genera, and for *Sphaeradenia* this reclassification is imminent (R. Eriksson, in press). *Dianthoveus*, the name an anagram of "Evodianthus," is a totally novel, monotypic genus.

This plant was first described and illustrated, as a short-stemmed terrestrial, in *The Flora of the Río Palenque Science Center* (Dodson & Gentry, 1978), where it was identified as *Asplundia vagans* Harl., a common root-climbing epiphyte of Central and South America. Examination of specimens of Cyclanthaceae in the herbarium at the Marie Selby Botanical Gardens, where vouchers for the Río Palenque florula are deposited, revealed that the plant was neither poorly illustrated nor a terrestrial form of *A. vagans*, but rather something problematic, exhibiting unusual characters of several genera. This stimulated two field trips to Ecuador, which, along with laboratory studies, convinced us that the plant is an undescribed genus.

MATERIALS AND METHODS

In total, well over 200 individuals in seven populations were examined in the field. Plants at various stages—from early anthesis through ripe infructescences to peduncle remains—were fixed in FAA for anatomical and morphological studies. Twenty-eight fluid-preserved collections at these stages were made, and numerous herbarium vouchers and live plants were collected. In the field, live specimens were examined to determine inflorescence position, presence/absence of latex, drying qualities of wounded and air-dried leaves, and features of leaf color and texture.

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[1] Supported by grants from the National Science Foundation (BSR-8508463) and the Jessie Noyes Smith Foundation to B. Hammel and a Grant-in-Aid to G. Wilder from the Cleveland State University. We thank Jack Fogerty, Mary Merello and Cheryl Roesel for technical assistance, John Myers for drawings, and Henk van der Werff for the Latin diagnosis. We thank Jorge Crisci, Michael Grayum, and W. John Kress for helpful discussion and criticism of an earlier draft of this paper and Gerrit Davidse and Lucinda McDade for critical review of the submitted manuscript.

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ANN. MISSOURI BOT. GARD. 76: 112–123. 1989.

Plants preserved in the field in FAA were drained of fluid and transported in sealed plastic bags within a large plastic container. Subsequently they were washed in water for several days and then stored in an aqueous solution of 5% glycerin and 50% ethanol. All measurements were taken from live or fluid-preserved plants at populations along the Río Pilatón (*Hammel & Wilder 16058, 16059, 16066, 16067 & 16074*). Leaf measurements were taken from a total of 17 adult leaves from three individuals. Inflorescence measurements were taken from four individuals, and flower measurements come from ten flowers in each inflorescence. Infructescence measurements were from ten individuals, and fruit measurements from ten fruits in each of four individuals. For anatomical studies, material of laminae, roots, and stems was prepared according to the methods of Wilder (1985). Seeds were taken from mature preserved infructescences embedded in Tissue Tek OTC polysaccharide compound, frozen, and sectioned in a cryostat. Sections were mounted, stained with toluidine blue, and viewed with a bright field microscope. Pollen was prepared with and without acetolysis and with and without critical point drying, coated with gold, and viewed with a Hitachi S45D scanning electron microscope. Detailed studies on the morphology and development of vegetative parts and inflorescences, and the anatomy of laminae, first-order roots, and rhizomes are in progress (Wilder, unpubl.).

In order to test our initial hypothesis of relationship of the new genus to *Evodianthus* we selected 22 characters for the 11 genera of Cyclanthaceae (Table 1), developed a character-by-taxon matrix (Table 2), and analyzed the data using PAUP for microcomputer, a maximum parsimony technique (Swofford, 1985). All characters were unweighted, but the four character states of "habit" were restricted to a specific order (Table 1 and discussion below). Since no logical basis was apparent for restricting the order of character transformations of other multistate characters, all other characters were treated as unordered. Characters with variable states for a particular genus were coded as missing (Pimentel & Riggins, 1987). Autapomorphies for each of the genera were not included in the analysis.

Collections made in December 1988 were added in proof and not considered in the counts and measurements.

TAXONOMY

Dianthoveus cremnophilus Hammel & Wilder, gen. et sp. nov. TYPE: Ecuador. Pichincha: Quito to Santo Domingo de los Colorados, Río Pilatón valley, 44 km E of Santo Domingo, on steep wet slope along highway, 0°23′S, 78°50′W, 1,200 m, 18 June 1987 (infr), *B. Hammel & G. Wilder 16058* (holotype, MO; isotypes, COL, DUKE, F, GB, NY, QCA, US).

TABLE 1. Characters and character states for the genera of Cyclanthaceae. Characters found only in one genus (autapomorphies) are not included.

A = Placentation: 0 = parietal, 1 = apical
B = Fruit fusion: 0 = some, 1 = none
C = Fruit type: 0 = other, 1 = succulent pixis
D = Seed shape: 0 = terete, 1 = moderately flattened, 2 = strongly flattened
E = Orientation of cells of testa: 0 = horizontal, 1 = vertical
F = Outer layer of testa with enlarged, dark cells: 0 = no, 1 = yes
G = Spinules on wall of inner layer of testa integument: 0 = no, 1 = yes
H = Inner tangential and radial walls of inner layer of integument equally much thickened: 0 = yes, 1 = no
I = Inflorescence position: 0 = terminal, 1 = lateral
J = Anther appendages: 0 = none, 1 = laminar-apiculate, 2 = globular
K = Phyllotaxis: 0 = distichous, 1 = spiral
L = Glands on staminate tepals: 0 = absent, 1 = present
M = Staminate flower symmetrical: 0 = yes, 1 = no
N = Staminate flower funnel-shaped: 0 = yes, 1 = no
O = Pollen: 0 = aperturate, 1 = inaperturate
P = Leaf styloids: 0 = unidirectional, 1 = omni, 2 = absent
Q = Birefringent cells in leaves: 0 = absent, 1 = present
R = Anthers: 0 = not sessile, 1 = sessile (no basal bulb or filament)
S = Habit:
  0 = terrestrial { a: 1 = epiphyte
  b: 1 = on rocks
  c: 1 = climber
T = Root styloids: 0 = absent, 1 = present
U = Circumstelar sclerenchymatous ring: 0 = absent, 1 = U-shaped, 2 = evenly thickened
V = Root stele nonperipheral phloem: 0 = in fascicles, 1 = dispersed
W = Spathe arrangement: 0 = dispersed, 1 = clustered

Evodianthi funiferi affinis sed habitu terrestre, statura majore, perianthо floris masculini uniseriato, tepalis acuminatis eglandulosisque, receptaculo plano, connectivo antherarum laminare apiculatoque, seminibus modice applanatis vel quasi teretis, perlongioribus quam latioribus differt. Ob receptaculi papillas multicellulares, formantes basibus staminorum cupulas, inter omnes Cyclanthaceas peculiaris.

TABLE 2. Data matrix for the 10 genera of subfamily Carludovicoideae with *Cyclanthus* as hypothetical ancestor. Characters coded ? were inapplicable or variable characters.

																			S					
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	a	b	c	T	U	V	W
Cyclanthus	0	?	0	0	0	0	0	0	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	0
Asplundia	0	0	1	2	?	0	0	1	1	0	1	1	?	?	0	0	0	0	0	0	?	0	1	0	0
Carludovica	0	0	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1
Dicranopygium	0	0	0	0	0	0	0	0	1	0	1	?	1	1	0	0	0	0	0	1	0	0	1	0	1
Evodianthus	0	1	0	2	1	0	0	1	0	0	1	1	0	0	1	1	0	1	0	0	1	1	2	1	1
Ludovia	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	2	1	0	?	0	?	0	1	0	0
Sphaeradenia	1	1	0	0	?	1	0	0	1	2	0	1	1	1	0	0	1	0	1	0	0	0	1	1	0
Stelestylis	1	0	1	0	?	1	0	0	1	2	0	1	1	1	0	0	1	0	1	0	0	0	1	1	0
Thoracocarpus	0	0	1	2	0	0	1	1	1	0	1	1	0	0	0	2	0	0	0	0	1	0	2	0	0
Dianthoveus	0	1	0	1	1	0	1	1	0	1	1	0	0	1	1	1	0	1	0	0	0	1	1	0	1
Schultesiophytum	0	1	0	1	1	1	0	0	1	1	1	1	0	1	0	2	0	0	0	0	0	0	0	0	1

Terrestrial herbaceous plant, often forming clumps by vegetative branching; the rhizomes 7–53 cm long, to about 6 cm diam. in mature specimens, often exposed and held erect by numerous stout, monomorphic, adventitious roots up to 75 cm long and 0.85 cm diam. Foliage leaves of adult plants 145–271.5 cm long, with spiral (dispersed, sensu Harling) phyllotaxy, crowded on the rhizome at internodes mostly less than 1 cm apart, eventually detaching and leaving the naked rhizome with well-defined leaf scars; sheaths 52–101 cm long, dull green and remaining intact; petioles 21–77 cm long; lamina unicostate or rarely and inconspicuously subtricostate, bifid to ½ or slightly less, 72–107 cm long, 16.5–30 cm wide at the base of the median sinus, the segments 9–16 cm wide; each half of the lamina with 19–26 folds, lanceolate with a short-acuminate tip, dark satiny green above, dull and paler below, scabrous when dry. Inflorescences solitary and terminal but becoming laterally displaced by the subtending, precociously expanding renewal bud. Peduncles 25–34 cm long at anthesis, becoming 41–61 cm long and curving down in mature fruiting stage, 1.4–1.8 cm diam. Spathes of two kinds, both persisting until very late flowering stage: 3 conspicuous spathes, thick, green and fleshy, differentiated into sheath, lamina, and sometimes petiole, 9.5–25.8 cm long, ca. 5–6 cm wide, ± clustered and inserted no more than 3 cm below the spadix, collectively surrounding the spadix, the lowermost much larger than the upper 2 and unusual in bearing petiolate and often bifid lamina; up to 6 inconspicuous spathes, comprising membranous greenish white scale leaves, up to 4.7 cm long and 1 cm wide, inserted above the conspicuous spathes and all ± at one level, usually subtending flowers and often inserted above the base of the spadix, arising only from one side of the inflorescence. Spadices cylindrical, at anthesis 7.8–9.5 cm long, 2.6–3.1 cm diam., sordid white, in ripe fruiting stage becoming 11–14.8 cm long, 4–6 cm diam., green. Staminate flowers ± obpyramidal, 3.3–5.5 mm long; receptacle approximately triangular in top view, ca. 2–3.3 mm wide, adorned with numerous multicellular papillae forming a cupule around the base of each anther; perianth lobes 10–18, thin and narrowly triangular-acuminate, (1–)1.3–2.7 mm long, eglandular, distributed ± evenly on the receptacle margin; stamens 19–32, the anthers ± elliptic but often widest above the middle, 0.7–1.1 mm long, 0.4–0.8 mm wide, the thecae occupying the lower ½–⅔ of the anther and separated by the broad upper portion of connective, this terminating in a laminar apiculate tip; filaments minute, 0.1–0.2 mm long or lacking; basal bulbs lacking. Pollen grains mostly ovoid but varying to nearly globose, 15–21.5 μm long, 14–15.5 μm wide, psilate, inaperturate. Pistillate flowers free to base, narrowly turbinate, at anthesis 3–3.5 mm long (from base

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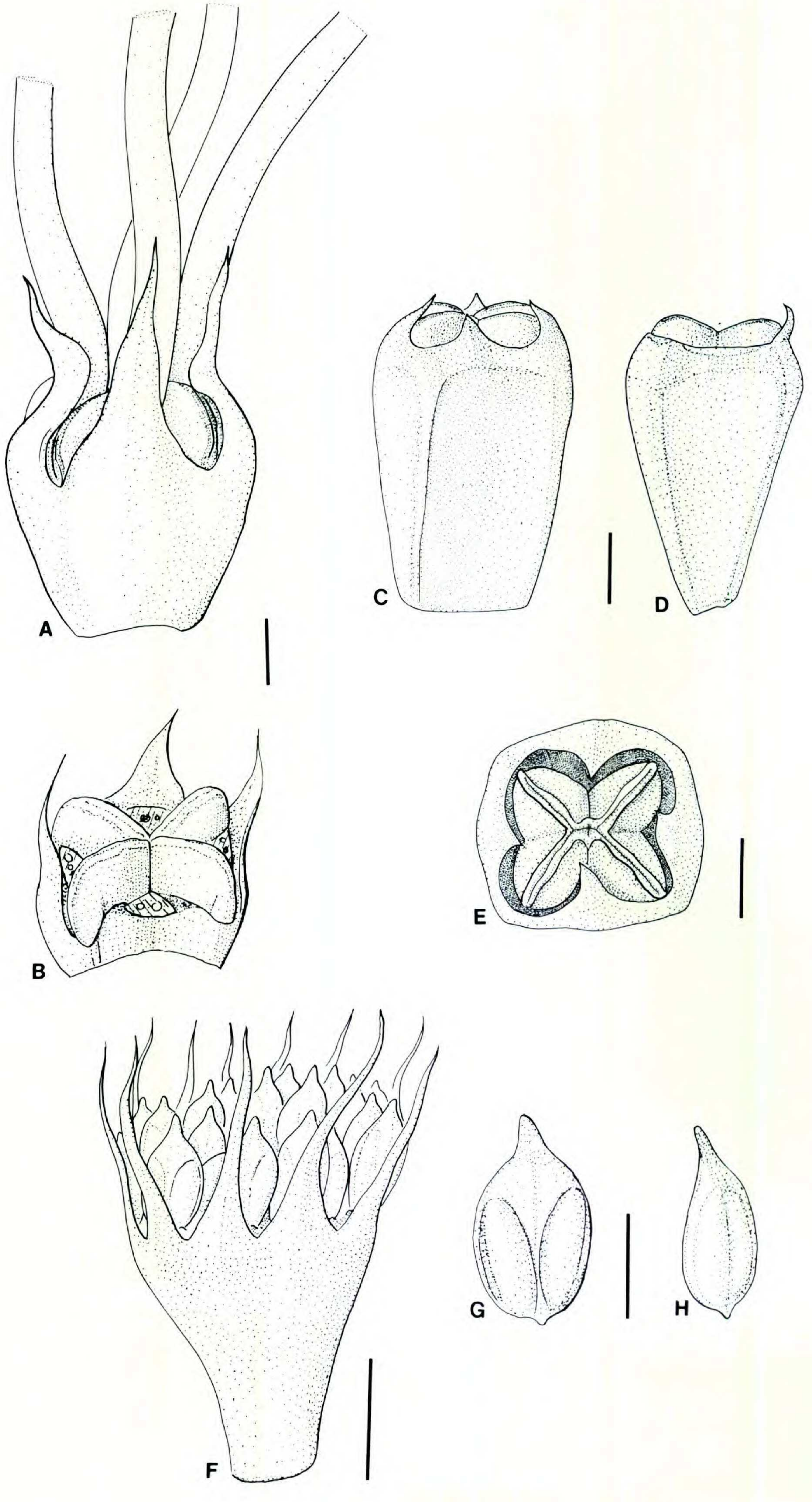
FIGURE 1. Flowers and fruits of *Dianthoveus cremnophilus*.—A, B. Young pistillate flowers, B with one tepal and all staminodia removed. Bar = 1 mm; *Hammel & Wilder 16066*.—C, D. Mature fruits, C viewed from side parallel to axis of spadix, D viewed from side perpendicular to axis of spadix. Bar = 5 mm; *Hammel & Wilder 16058*.—E. Mature fruit, top view. Bar = 5 mm; *Hammel & Wilder 16058*.—F. Staminate flower. Bar = 1 mm; *Hammel & Wilder 16067*.—G, H. Anthers, front view (G) and side view (H). Bar = 0.5 mm; *Hammel & Wilder 16067*.


A
B
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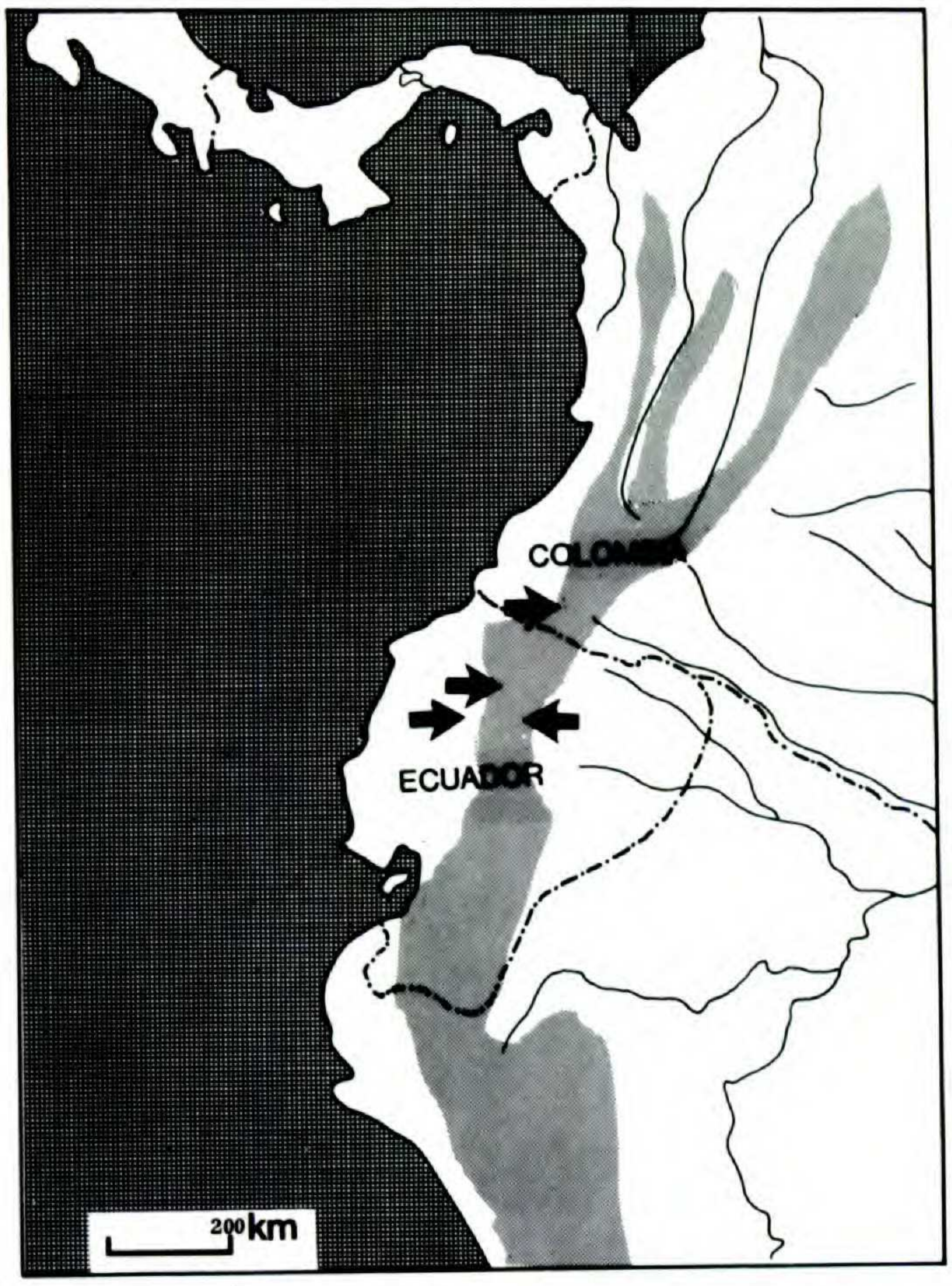


FIGURE 2. Distribution of *Dianthoveus cremnophilus.*

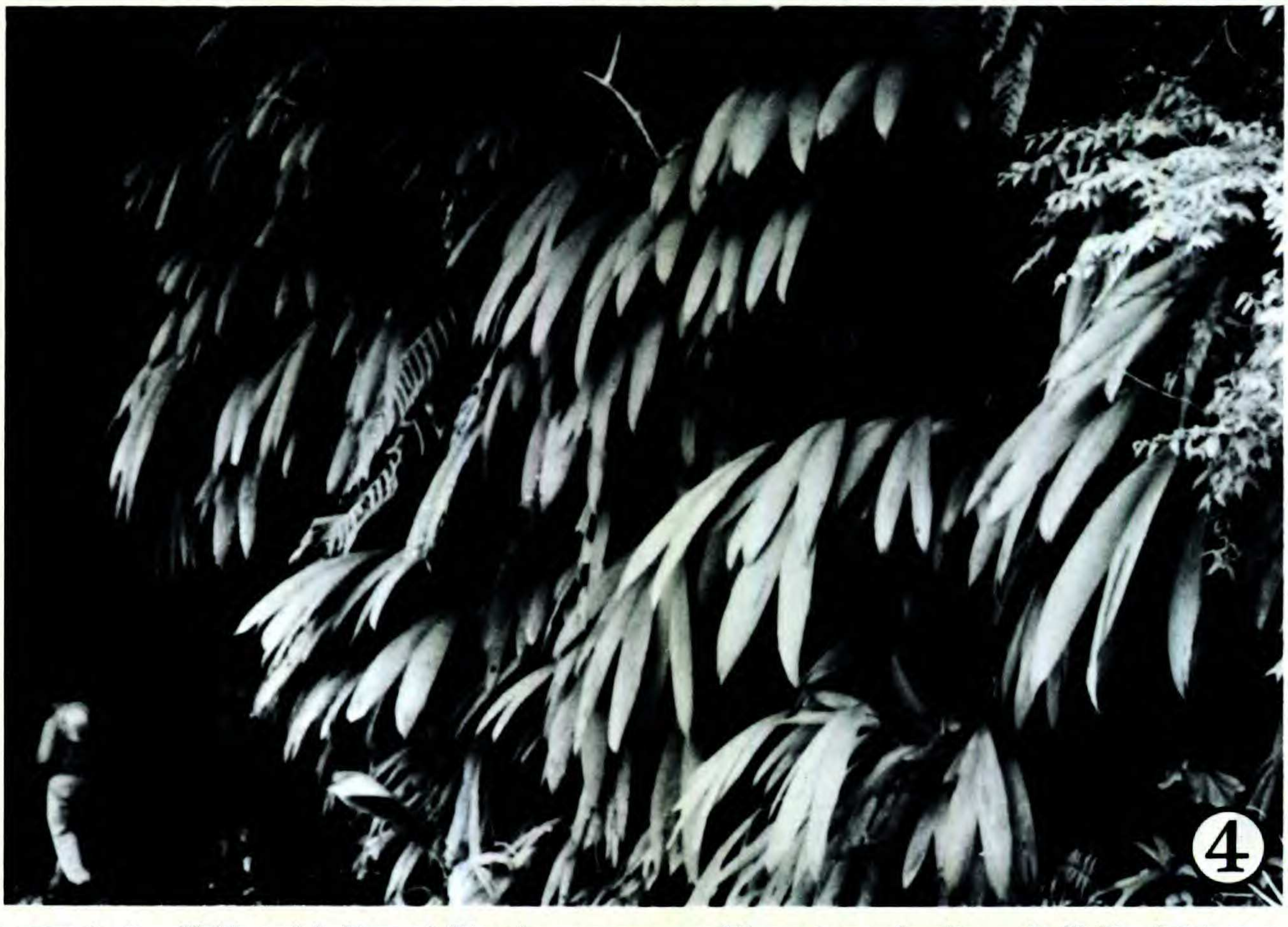
to top of stigma), 3.8–4.1 mm wide, at ripe fruiting stage becoming 2.1–2.4 cm long, 1.5–1.7 cm wide, green at maturity; tepals free to base (partially connate in age), arising from the top of the inferior ovary, long-acuminate, the tips folding over the stigmas and then curving out, at anthesis 2–4.3 mm long, 2–4.3 mm wide, in fruiting stages the tips often breaking off, becoming acute to rounded, 1.5–3.2 mm long, 4.5–9.5 mm wide; staminodia white, to ca. 9.5 cm long, ca. 1.5 mm diam., the distal ends apiculate, relatively flattened and attenuated but otherwise identical to an anther; styles at anthesis 0.9–2 mm tall, in fruiting stages 1–2.5 mm tall; stigmas convex in side view and slightly uncinate, extending between the tepals, at anthesis 1.2–3 mm long, 0.7–2 mm wide, in mature fruiting stages 3.5–4.2 mm long, 2–3.7 mm wide; stigmatic crest seen from above linear, papillate and sometimes sulcate; placentae 4, parietal. Seeds fusiform but moderately flattened, 1.4–2.45 mm long, 0.3–0.6 mm wide, dark amber-colored; seed coat with tannin and mucus; embryo lacking starch. Figure 1.

Distribution and habitat. Known only from wet forest in the Andean foothills of southwestern Colombia and northern Ecuador. In Colombia the species has been found only on the Pacific slope at mid elevations, but in Ecuador it is known from between 150 to 1,200 m elevation and occurs on both sides of the Andes.

Paratypes. COLOMBIA. NARIÑO: road from El Espino to Tumaco, ca. 16 km W of Ricaurte, 850 m, 18 Nov. 1986 (sterile), *B. Hammel & R. Bernal 15735* (MO); 7 Dec. 1988 (infr), *B. Hammel 17135* (COL, MO). ECUADOR. LOS RÍOS: between Santo Domingo and Quevedo, Centinela ridge, 13 km E of Patricia Pilar, 300 m, 1 Dec. 1986 (infr), *B. Hammel & J. Trainer 15846* (MO); Río Palenque Science Center, 2 km S of Patricia Pilar, common plant on creek bank, 150–220 m, 5–14 Mar. 1977 (young infr), *C. Dodson 6645* (SEL); 19 July–11 Aug. 1977 (old infl and young infr), *C. & H. Dodson 6730* (SEL); 30 Nov. 1986 (infr), *B. Hammel & C. Dodson 15845* (MO); 18 Nov. 1979 (sterile), *Schupp 50* (SEL). NAPO: new road to Loreto, 18 km E of junction with Baeza-Tena Road, 1,200 m, 21 Dec. 1988 (infr), *B. Hammel & G. Wilder 17272* (COL, MO, QCA, NY); Baeza to Tena, ca. 58 km S of Baeza, ca. 1,200 m, 17 Dec. 1986 (sterile), *B. Hammel 15971* (MO); Tena to Puyo, 3 km S of Tena, 500 m (sterile), *B. Hammel 16017* (MO). PICHINCHA: Reserva ENDESA, km 113 on Quito to Puerto Quito road, 450 m, 16 Dec. 1988 (infr), *B. Hammel & G. Wilder 17234* (GB, MO, PSO, QCA); Santo Domingo de los Colorados to Quito, Río Pilatón valley, 13 km E of Santo Domingo, Tinalandia resort, on steep slope along stream in forest, 800 m, 30 Nov. 1986 (old infl and young infr), *B. Hammel & J. Trainer 15820* (CAS, K, MO, US); 20 June 1987 (infl), *B. Hammel & G. Wilder 16066* (MO); (infl and infr), *B. Hammel & G. Wilder 16067* (COL, F, MO, QCA); 18 km E of Santo Domingo, on vertical slope just behind CEPE gas station, 750 m, 22 June 1987 (infl), *B. Hammel & G. Wilder 16080* (MO, US); 32 km E of Santo Domingo, N of highway and Río Pilatón, 850 m, 19 June 1987 (infl), *B. Hammel & G. Wilder 16059* (MO); 34.5 km E of Santo Domingo, on steep slopes S of highway, 1,100 m, 21 June 1987 (infl and infr), *B. Hammel & G. Wilder 16074* (COL, GB, GH, MO, QCA); same locality as type, 6 Dec. 1986 (infr), *B. Hammel & J. Trainer 15890* (MO, SEL).

Dianthoveus cremnophilus is robust, short-stemmed, and terrestrial (Fig. 3) but, as indicated by its epithet, it is a "cliff-loving" plant (Fig. 4). At many of the sites along the Río Pilatón we were able to collect plants only by pulling ourselves up nearly vertical slopes, using roots and stems as hand holds. Several large populations, including the type, were growing on dripping and mossy rock walls. All of the sites were along small streams or gullies or on wet, shaded slopes in isolated patches of relatively undisturbed forest. Even at Río Palenque, where the terrain is essentially a rolling plain, plants occur only on steep banks along small streams in the forest. Plants at two of the sites had been exposed by recent felling of forest cover and showed signs of sun damage.

Although *Dianthoveus* is locally abundant and probably formerly occurred throughout the wet lowlands and foothills of the Andes in northern



FIGURES 3, 4. Habit and habitat of *Dianthoveus cremnophilus*, at type locality.—3. Habit; divisions on tape are 10 cm each.—4. Habitat; plants were often abundant on wet, vertical slopes.

Ecuador, it seems not to occur outside of that area. Attempts to find it have failed on the Amazonian side of the Andes in southern Colombia near Mocoa in Putumayo Province, and in the Pacific lowlands of southern Colombia (near Barbacoas) in habitat similar to that of the adjacent Ecuadorian localities.

Phenology. Nearly all of the collections of *Dianthoveus* have been made from June through December, which spans the primary dry season for humid areas of northwestern Ecuador (Dodson & Gentry, 1978). Our search of numerous large populations at five different localities during June revealed four phenological classes: (1) most plants bore no outward sign of fertile structures (N = ca. 200) except for some with old peduncle stubs; (2) next most abundant were plants with remnants of old infructescences, primarily long-rotten peduncles (N = ca. 30); (3) we saw and collected only 12 individuals with young to mature infructescences, and (4) five individuals with immature to old inflorescences. At the type locality, only fruiting plants were observed in December of 1986 and in June of 1987. The single mid wet season collection has a young infructescence. Individuals apparently bear a single inflorescence per rhizome at one time. Our studies suggest that *Dianthoveus* flowers and fruits sporadically throughout the year. From the relatively frequent plants with peduncle remnants during June, we infer a somewhat higher flowering frequency during January through March, i.e., in the middle of the rainy season, a common pattern in other Cyclanthaceae.

Development and morphology of fertile structures. The peduncles are most flexible at the base and are held erect at anthesis by the tightly overlapping leaf sheaths. Later, as the infructescence becomes heavier, the elongating peduncle bends so that the mature infructescence is held either horizontally or nearly pendent. The peduncle is persistent long after the fruits have been shed, and plants are often found with the fibrous remains of peduncle firmly attached to the rhizome. Both conspicuous and inconspicuous spathes persist into very late flowering stage with the largest, lowermost spathe persisting longest. Spathe scars are indistinct.

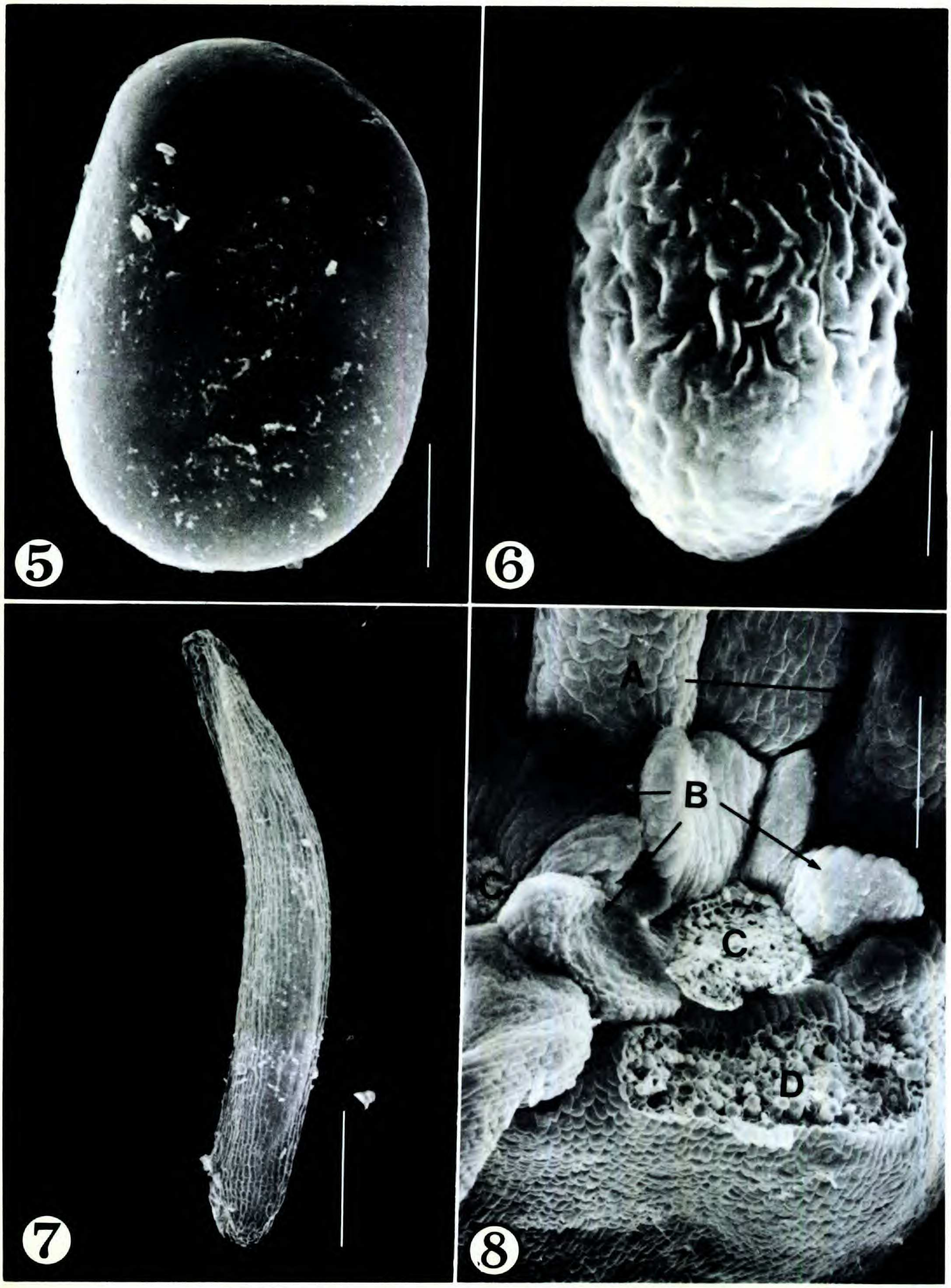
The fruits of *Dianthoveus* remain green or become light brown at maturity and apparently offer little attraction to dispersers; they are neither fragrant nor very juicy. We found seeds germinating in the debris of an old infructescence at the base of a plant, and often seedlings were found on wet rock walls below the mother plants. Such gravity or "flush dispersal" is probably usual for the genus; however, we found several fruits on one infructescence with the distinctive prints of bat teeth. In *Evodianthus* the berries become bright pale orange and very juicy at maturity and are undoubtedly dispersed by birds or bats.

Staminate flowers are tightly crowded among the pistillate flowers throughout development and persist into the early stages of fruiting; remains of the pedicels can be found even among mature fruits. Tepals often vary in length within one flower and usually with a tendency for the longest tepals to be together, making the flower slightly asymmetrical. This asymmetry, however, appears to be random with respect to the associated pistillate flower; the longest tepals, for example, may or may not face the pistillate flower. The tepals are thin and become brown at anthesis. They are always without resin glandules.

Tepals of the pistillate flowers are quite similar in shape and texture to those of the staminate flowers, an unusual condition for the family. Their apices are thin, nearly filamentous, and at first lie closely appressed to the stigmas and to the staminodia. In fruiting stages the tepals become much broader—only acute to rounded—and the tips often break off, leaving an irregular ridge around the stigmas, which no longer protrude and are often turned upward rather than uncinate. The sides of the fruit converge basally towards the long axis of the spadix into a narrow, vertical, lenticular shape.

Relationships. A simple comparison of the new genus with others in the family suggests that it is closely related to *Evodianthus*. Most notably, both genera and no others have leaves that are scabrous when dry. Anatomically, this translates into "styloid sacs [which] are normally elongated in all directions within the mesophyll, routinely crossing cell layers" (Wilder, 1985). All other Cyclanthaceae with styloid sacs have them elongated only parallel to the longitudinal files of parenchyma cells and confined to one layer. Only *Evodianthus* and *Dianthoveus* have styloid sacs in roots. Pollen of both genera is the smallest in the family and inaperturate (Figs. 5, 6), in contrast to the aperturate pollen of all other genera. Both genera have very short or no filaments and lack basal bulbs. Both have unicostate or cryptically subtricostate leaves, separate fruits, symmetrical staminate flowers, and terminal inflorescences, characters unusual in the family but shared with other genera (Table 3).

Features of staminate flowers and seeds have been especially important for delimiting supraspecific taxa within the Cyclanthaceae (Gleason,



FIGURES 5–8.—5. Pollen of *Dianthoveus cremnophilus*. Bar = 5 μm; *Hammel & Wilder 16067*.—6. Pollen of *Evodianthus funifer*. Bar = 5 μm.—7. Seed of *Dianthoveus cremnophilus*. Bar = 0.5 mm; *Hammel & Wilder 16058*.—8. Receptacle of staminate flower of *Dianthoveus cremnophilus*. A = base of anthers; B = cupule-forming papillae; C = point of attachment of stamen; D = point of attachment of tepal. Bar = 0.2 mm; *Hammel & Wilder 16067*.

TABLE 3. Hierarchy of unusual characters of *Dianthoveus* and the genera sharing them.

Character	Shared with
Papillate receptacles	none
Long-acuminate tepals	none
Inconspicuous spathes	*Cyclanthus*
Eglandular staminate tepals	*Dicranopygium* subg. *Gleasonianthus*
Apiculate anther appendages	*Schultesiophytum*
Scabrous leaves	*Evodianthus*
Styloids in roots	*Evodianthus*
Inaperturate pollen grains	*Evodianthus*
Sessile anthers	*Evodianthus*
Spinules on wall of seed coat	*Carludovica*, *Thoracocarpus*
Moderately flattened seeds	*Carludovica*, *Schultesiophytum*
Separate fruits	*Evodianthus*, *Schultesiophytum*, *Sphaeradenia*
Terminal inflorescences	*Evodianthus*, *Carludovica*, *Cyclanthus*
Clustered spathes	*Evodianthus*, *Carludovica*, *Schultesiophytum*, *Dicranopygium*

1929; Harling, 1958; Wilder, 1978). In the new genus, characters of both these structures differ markedly from those of *Evodianthus*, from which the former differs by its lack of a biseriate perianth (unique to *Evodianthus*), its lack of a funnelform receptacle in the staminate flowers (found in *Evodianthus* and several other genera), and by its only moderately flattened and narrowly elliptic seeds (Fig. 7). *Evodianthus*, as well as *Asplundia* and *Thoracocarpus*, have broadly elliptic, strongly flattened seeds. The seed coat structure also differs markedly from that of *Evodianthus* (see below). The new genus is further distinguished by the eglandular, acuminate tepals of the staminate flowers (which are similar only to those of *Dicranopygium* subgenus *Gleasonianthus*), the apiculate laminar appendages of the anthers (shared only with *Schultesiophytum*), and especially the peculiar papillate receptacle of the staminate flowers (Fig. 8).

Seed coat structure is variable among genera of Cyclanthaceae and was an important consideration in Harling's delimitation of genera in the family. We have interpreted the wall layers by focusing on the inner and outer cuticles, described by Harling and present in all genera. The seed coat of *Dianthoveus* (Fig. 9) is similar to those of *Carludovica* and *Thoracocarpus*; the innermost layer of the outer integument in all three genera has relatively large thin-walled cells with spinulose wall ingrowths on the inner tangential walls, whereas *Evodianthus* lacks these spinules (Harling, 1958: 38–43).

Evodianthus occurs rarely as a terrestrial plant and rarely with leaf blades nearly as large as those of the new genus. With fresh material, the less glossy (more satiny) aspect of the upper leaf surface, the larger size, and constantly terrestrial and short-stemmed habit of *Dianthoveus* distinguish it vegetatively from *Evodianthus*. Due to the similarity of these two genera, *Evodianthus* specimens (and all other Cyclanthaceae) at COL, F, MO, QCA, and SEL were examined to see if the new genus was included among them; it was not.

PHYLOGENETIC ANALYSIS

The Cyclanthaceae are widely considered to be monophyletic (Dahlgren et al., 1985; French et al., 1983), and for the most part each of the 11 genera also has at least one clear apomorphy supporting its monophyly. Within Cyclanthaceae, *Cyclanthus* possesses many unique and highly derived features (Dahlgren et al., 1985; Harling, 1958; Wilder & Harris, 1982) and apparently shares only ancestral characters with other genera. The similarity of seeds of *Cyclanthus* to those of Pan-

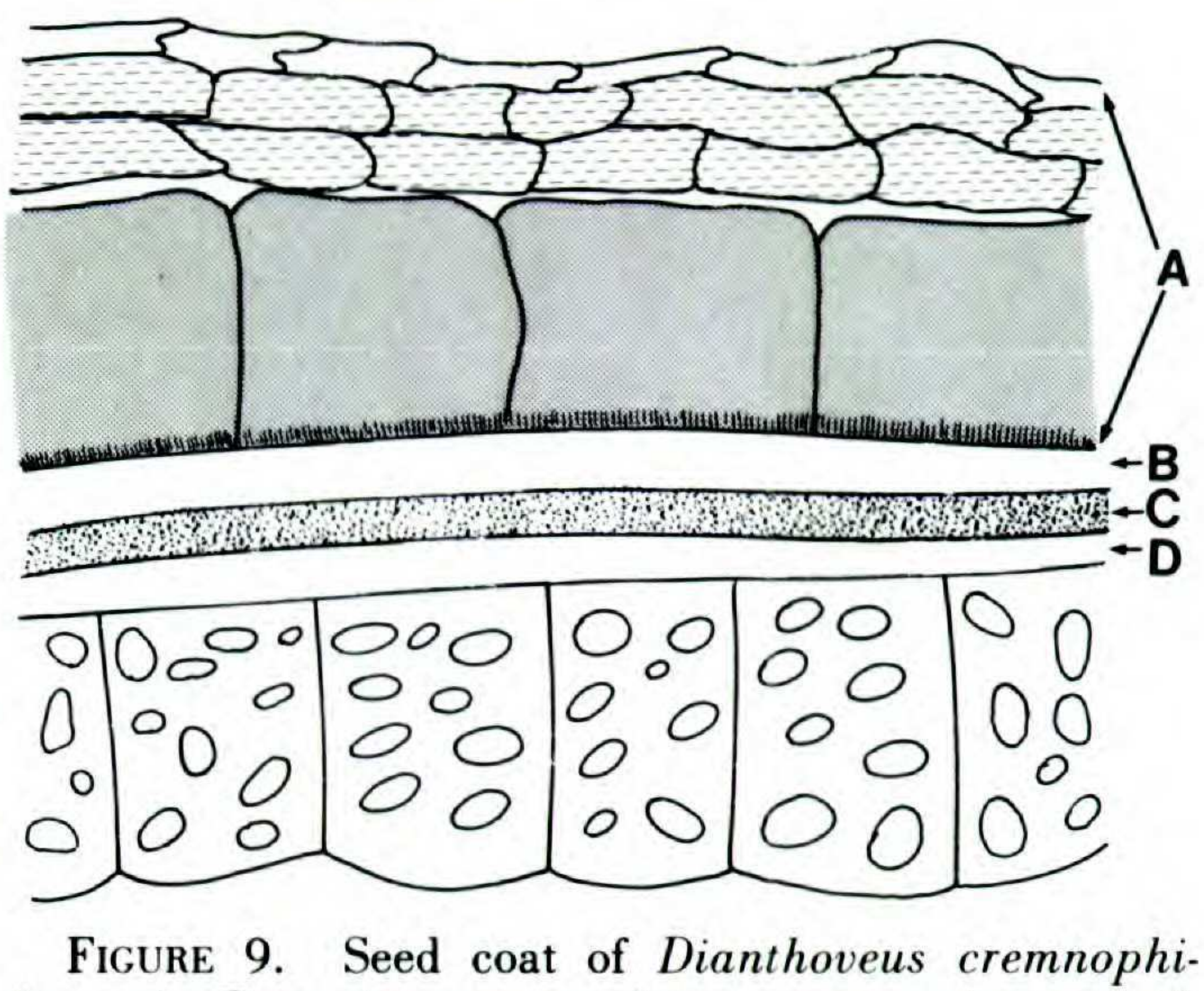


FIGURE 9. Seed coat of *Dianthoveus cremnophilus*.—A. Outer integument; lower arrow points to spinulose wall ingrowths.—B. Outer cuticle.—C. Inner integument.—D. Inner cuticle; *Hammel & Wilder 16058.*

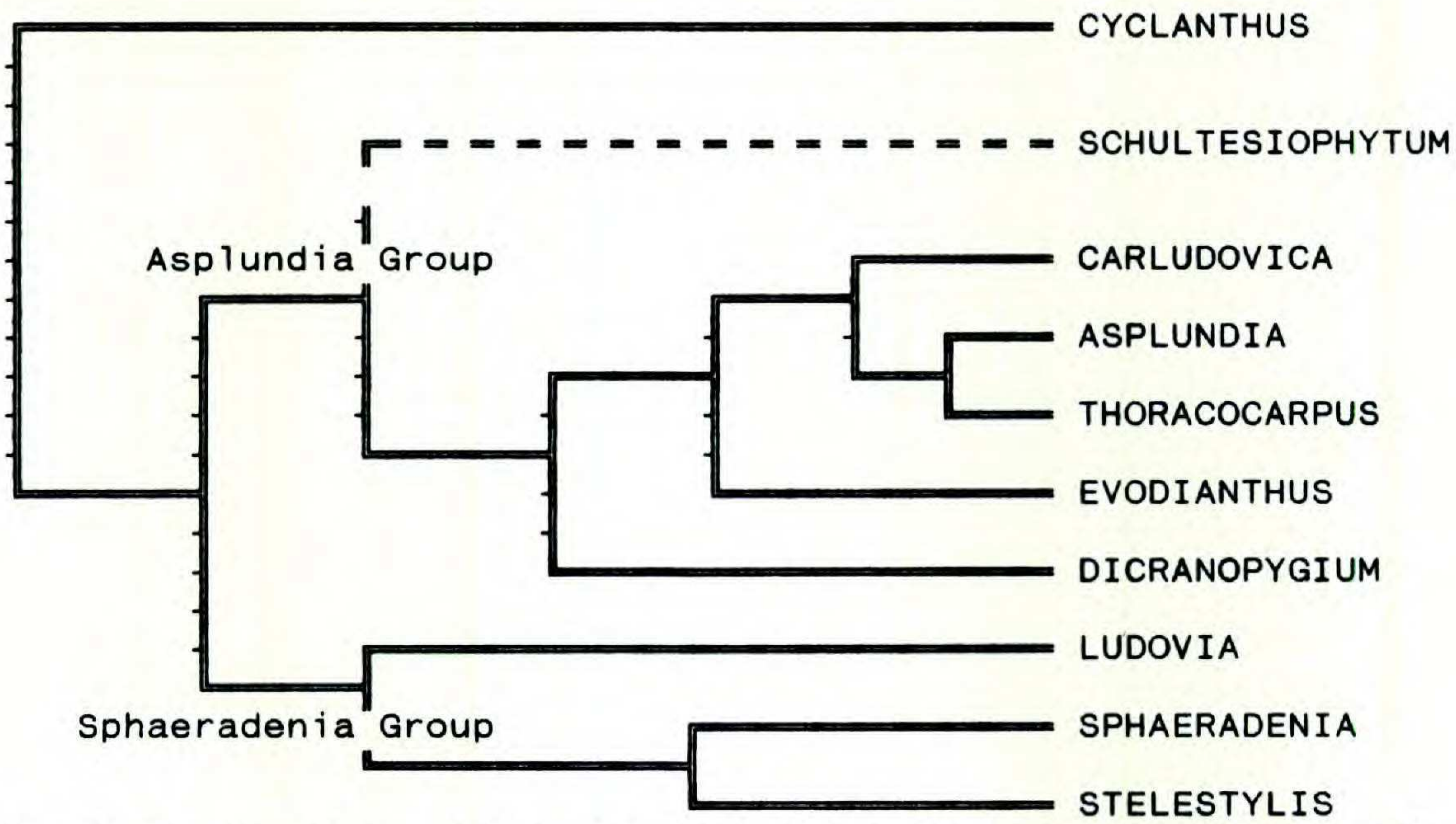


FIGURE 10. Phylogenetic scheme of Cyclanthaceae. Dashed line is Harling's convention for indicating highly uncertain position of *Schultesiophytum*—staminate flowers were unknown. Adapted from Harling (1958).

danaceae, especially in the genus *Freycinetia*, figured strongly in Harling's "geneological tree" (1958) for the genera of Cyclanthaceae (Fig. 10), including division of the family into two subfamilies. Furthermore, a preliminary analysis using *Freycinetia* (Pandanaceae) as the outgroup resulted in three trees, all of which supported the Cyclanthoideae/Carludovicoideae subdivision of the family (Hammel, unpubl.).

Thus, as a starting point we accepted a sister group relationship for the two subfamilies of Cyclanthaceae and postulated hypothetical ancestor for the Carludovicoideae based on the presumably ancestral characters of *Cyclanthus*, the only genus in the Cyclanthoideae. *Cyclanthus* contains only two species and is monomorphic for the characters analyzed; variability within the hypothetical ancestor was therefore not a problem. Characters not obviously comparable between the two subfamilies, e.g., floral symmetry (*Cyclanthus* lacks distinct, meristic floral units at maturity) were coded either by looking outside the family to the Araceae, Arecaceae, and Pandanaceae, where Harling and others have indicated the most likely affinity with the Cyclanthaceae, or by designating them as missing characters for *Cyclanthus*.

Harling's (1958) proposed relationships among genera in his "*Asplundia* group," which would include the new genus, by his own admission were quite tentative (Fig. 10). The main purpose of our analysis was to make an explicit statement as to the placement of *Dianthoveus* within the family, using characters from Harling and new characters. Discussion of those aspects of the character analysis not directly pertinent to the new genus and comparison of the phylogeny produced with these methods to that of Harling will be presented elsewhere (Hammel, unpubl.).

Character coding. Several characters were coded as missing in *Cyclanthus*, the hypothetical ancestor for this analysis. For example, although the pistillate "units" seem to demonstrate a remarkable extreme of fusion among parts, they readily dehisce from each other at maturity. Furthermore, it is difficult to judge an immediate ancestral state for this character from outgroup comparison; fruits are commonly fused in Pandanaceae, rarely in Araceae, and sometimes in Arecaceae. Note also that whereas Dahlgren & Rasmussen (1983) cited "indehiscent fruits" as a possible synapomorphy for their Areciflorae complex (Arecaceae, Cyclanthaceae, Pandanaceae), the berries in most species of Cyclanthaceae are dehiscent by apical caps (*Thoracocarpus*, all but one species of *Asplundia*, and most species of the *Sphaeradenia* group; Hammel, unpubl.). Live, mature infructescences of Pandanaceae, especially *Freycinetia*, need to be examined for comparison.

Characters of the staminate flowers were likewise difficult to polarize with reference to *Cyclanthus*, which at maturity has only amerous rows of stamens. Pandanaceae also have amerous and apetalous staminate inflorescences. Flowers were coded as primitively symmetrical by reference to Araceae and Arecaceae. Presence/absence of glands on tepals and shape of perianth were coded as missing data.

The phyllotaxy in *Cyclanthus* is spirodistichous (Wilder, 1981), making the coding of this char-

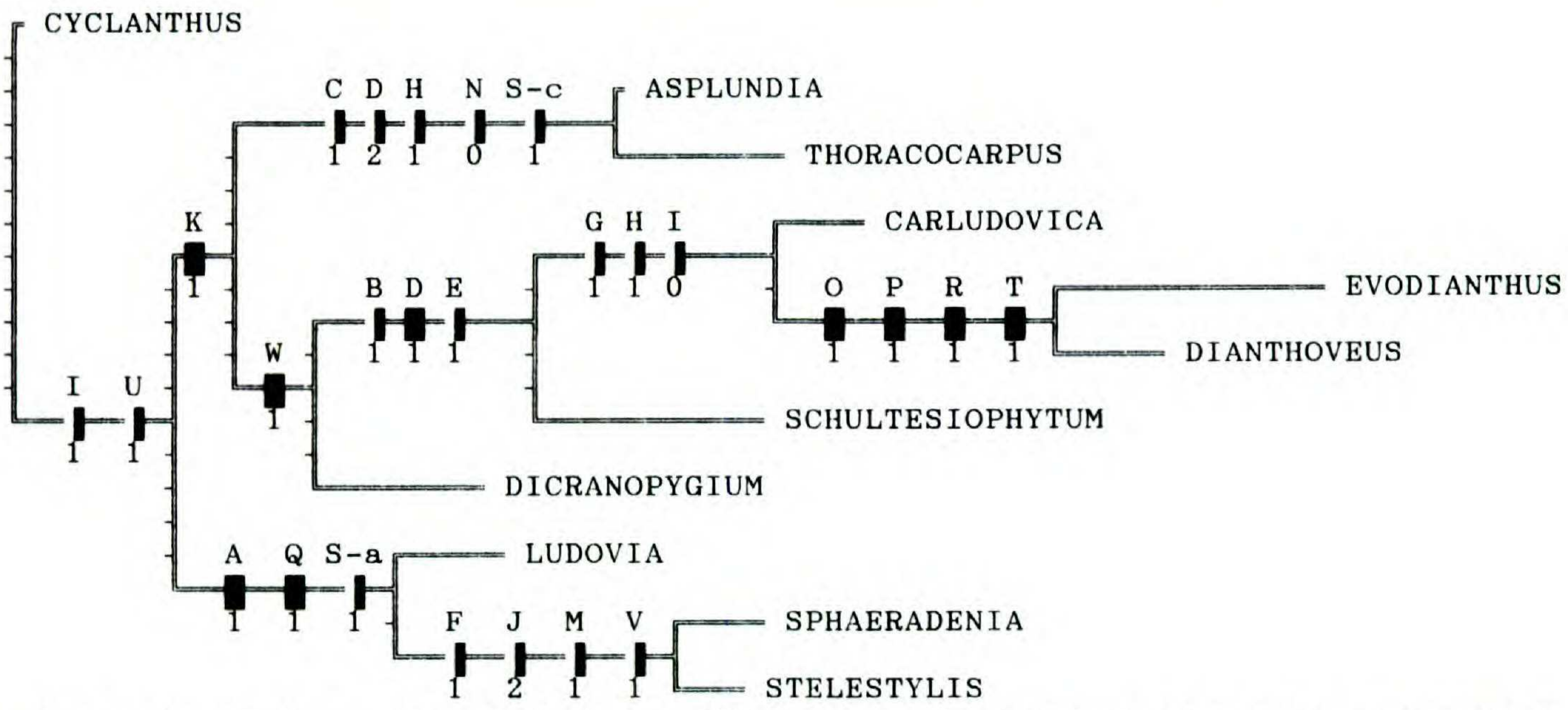


FIGURE 11. Cladogram of the Cyclanthaceae. Wide bars are uniquely derived and consistent synapomorphies; half-bars are synapomorphies of character states found elsewhere in the family or reversed within the defined group. Letters above bars refer to characters (Table 1), numbers below to character states. Length of terminal clade is directly related to number of apomorphies discovered by analysis. Length = 48; consistency index = 0.604; originally known autapomorphies not included in analysis.

acter problematic; genera of the Carludovicoideae have either orthodistichous (in a few species spirodistichous) or spiral phyllotaxy. The Pandanaceae have tristichous phyllotaxy. For this analysis spiro- and orthodistichy were both subsumed under the category "distichous," and phyllotaxy was coded as having only two states. The terminal inflorescences of *Cyclanthus* seem well supported as ancestral; terminal inflorescences are the rule in Araceae (Ray, 1987 and pers. comm.) and in Pandanaceae (Tomlinson & Wilder, 1984) and are characteristic of the "primitive" coryphoid palms. In palms, however, terminal inflorescences are never evicted by axillary shoots (Tomlinson & Wilder, 1984). States for seed characters were coded directly from *Cyclanthus* as ancestral; the similarity of seeds of *Cyclanthus*, *Dicranopygium*, and *Ludovia* with those of some members of the Pandanaceae is one of the main features that Harling (1958) saw as indicating a close relationship between Pandanaceae and Cyclanthaceae.

The branched order of character states for "habit" (Table 1) is rationalized by the observation that variable taxa almost always include terrestrial members. It then seems unlikely that any nonterrestrial form was derived one from another.

RESULTS AND DISCUSSION

From our data matrix (Table 2), PAUP found five trees with 49 steps and a single most parsimonious cladogram with 48 steps (Fig. 11). A sister-group relationship between *Dianthoveus* and *Evodianthus* is supported by all of these analyses. Furthermore, when the data matrix is changed to accommodate different possibilities for states coded as "missing" or different interpretations of problematic characters for the hypothetical ancestor, such as fruit fusion and phyllotaxy, this relationship remains unchanged even when the overall topology changes.

The highly corroborated sister-group relationship between *Evodianthus* and *Dianthoveus* allows a rational discussion of homologies of the unusual staminate flowers in the new genus. On the basis of our hypothesis (Fig. 11), *Dianthoveus* appears to retain more relatively primitive character states than *Evodianthus*, such as the terrestrial (vs. climbing) habit. The moderately flattened seeds are also relatively primitive as compared with the strongly flattened seeds of *Evodianthus*. The laminar-apiculate anther appendages of *Dianthoveus* could be symplesiomorphous with those of *Schultesiophytum*, but that assumption would require an additional step; it is more parsimonious to assume that this kind of anther evolved independently in the two genera. The biseriate perianth of *Evodianthus*—an apomorphy for *Evodianthus* not included in the analysis—appears to be derived within the family.

From this basis we can argue that the inner cycle of the biseriate perianth of *Evodianthus* might be an elaboration of the unusual papillate receptacle of *Dianthoveus*. By this hypothesis, the lobes of the inner perianth of *Evodianthus* are not appendicular organs (leaf homologues), but rather emergences, equivalent developmentally to the papillae, which compose cupules in *Dianthoveus*.

In all cases, regardless of coding, eglandular staminate tepals appear to have arisen twice within the Carludovicoideae—in *Dicranopygium* subgenus *Gleasonianthus* and in *Dianthoveus*. However, according to Harling (1958; see also Wilder, 1978), the eglandular tepals of subgenus *Gleasonianthus* are not "real perianths," but rather are homologous with stamen filaments; he found that lobes of this "false perianth" sometimes bear reduced anthers. In addition, the filaments of anthers in subgenus *Gleasonianthus* are somewhat flattened and acute, resembling the lobes of the false perianth. In *Dianthoveus* we see no equivalent basis for hypothesizing a staminodial nature for the eglandular tepals. We found none with reduced anthers, and they certainly bear no resemblance to filaments of stamens (*Dianthoveus* lacks filaments). Based on their position, they appear simply to be homologous with the glandular outer whorl of the biseriate perianth of *Evodianthus* and the "real perianth" of other Cyclanthaceae. Under this reasoning, the eglandular tepals of *Dianthoveus* are similar to those of *Dicranopygium* subgenus *Gleasonianthus* only by convergence.

CONCLUSION

Before our cladogram or any other is presented as a phylogeny for the family, several of the characters and character states need to be re-evaluated and the hypothesis tested with additional characters. For example, the character of spathe position, crucial for placing *Dicranopygium* in the clade definied by clustered spathes, is somewhat subjective. The spathes of *Carludovica*, *Schultesiophytum*, and *Dianthoveus* are not much closer together than many species outside the clade. Which other, if any, multistate characters (e.g., seed shape) might logically be ordered? One also wonders if characters such as inflorescence position and phyllotaxy, which seem to encompass a large suite of characters, should be given extra weight or broken into several characters. All of this needs to be evaluated within the context of a hypothetical ancestor postulated on the basis of taxa outside the Cyclanthaceae.

Although a close relationship between *Dianthoveus* and *Evodianthus* was suggested initially by the observation that only these two have scabrous leaves, a phylogenetic analysis using parsimony demonstrates the hypothesis as supported by numerous characters. It also provides a logical basis for suggesting the evolutionary homologies of the unusual floral features of the new genus, in particular, the papillate receptacle (possibly homologous with the inner perianth of *Evodianthus*), the laminar apiculate anthers (evolved in parallel to those of *Schultesiophytum*), and the eglandular tepals (convergent with those of *Dicranopygium* subgenus *Gleasonianthus*).

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